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Maternal Condition and Facultative Sex Ratios in Populations with Overlapping Generations

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ABSTRACT: Facultative investment in offspring sex is related to maternal condition in many organisms. In mammals, empirical support for condition-dependent sex allocation is equivocal, and there is some doubt as to theoretical expectations. Much theory has been developed to make predictions for condition-dependent sex ratios in populations with discrete generations. However, the extension of these predictions to populations with overlapping generations (OLGs; e.g., mammals) has been limited, leaving doubt as to the specific prediction for maternal-condition-dependent sex ratios in mammals. We develop a population genetics model that incorporates maternal effects on multiple offspring fitness components in a population with OLGs. Using a rare-gene and evolutionarily stable strategy approach, we demonstrate that sex ratio predictions of this model are identical to those for equivalent discrete generations models. We show that the predicted sex ratios depend on the sex-specific ratio of R_0 (offspring lifetime fitness) for offspring of good and poor mothers. This offspring lifetime fitness rule indicates that empirical research on conditional sex ratios should consider all three components of offspring R_0 (juvenile survival, adult life span, and fertility).

Keywords: Trivers-Willard model, Charnov-Bull model, mammal sex ratios, overlapping generations, population genetics model.

Trivers and Willard (1973) first proposed that a mother may allocate to offspring of different sexes according to her condition. They suggested that in a polygynous mating system, reproductive success is highly skewed in males compared with females—only the few best males secure

reproductive opportunities. In such a system, a mother that is going to bear reproductively competitive offspring should have sons, assuming that she can alter sex ratio without compromising other fitness components (e.g., litter size). The model assumes that maternal condition affects offspring condition, that offspring condition is maintained until adulthood, and that offspring condition has a greater effect on a son's reproductive success than on that of a daughter. Reproductive competitive ability is the measure of offspring fitness in the Trivers-Willard (T-W) hypothesis.

Stimulated by the T-W ideas, Charnov and Bull (1977) extended the principle (condition-dependent male/female fitness effects should select for facultative sex ratios) to a wide variety of contexts (overviews in Charnov 1982, 1993). It was also soon realized that Ghiselin's (1969) size-advantage hypothesis for sex reversal made very similar male/female fitness assumptions. There is now a large literature on condition-dependent sex ratios in diverse organisms (see, e.g., de Jong and Klinkhamer 2005 for plants).

Although the T-W hypothesis was developed with ungulate mammals in mind, subsequent application of the model to mammals has led to inconsistent results (e.g., Hewison and Gaillard 1999; Cockburn et al. 2002; Sheldon and West 2004). While compelling examples of condition-dependent biases in offspring sex exist in mammals (e.g., Clutton-Brock et al. 1986; Cameron et al. 1999; Fisher 1999), support for the T-W hypothesis is often unclear in specific studies or when considering the results of such studies in aggregate. In some species, sex ratio biases are related to maternal condition, but the assumptions of the T-W hypothesis have not been tested (Hewison and Gaillard 1999). In other species, the assumptions of the model appear to be met, but no conditional sex ratio biases are observed (Krackow 1997; Bercovitch et al. 2000; Blanchard et al. 2005). Recent reviews of sex ratios in mammals (and birds) have substantially advanced our understanding of the diverse empirical results by highlighting the potential constraints on sex ratio adjustment, the interaction of multiple selective agents, and the proper measures of maternal

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condition (Cockburn et al. 2002; West and Sheldon 2002; Cameron 2004; Sheldon and West 2004; West et al. 2005). Many inconsistencies in studies of the T-W hypothesis may be attributed to a mismatch between theory and empiricism. That is, potentially, predictions are not met because of insufficient knowledge of the biology of the organisms (e.g., offspring fitness components) and how it relates to theoretical foundations. Alternatively, it may be because models do not explicitly take into account the complicated life histories of long-lived animals with overlapping generations (OLGs; Frank 1990; Pen and Weissing 2002).

Previous theoretical work on condition-dependent sex ratios has applied game theory (evolutionarily stable strategies) to population genetic models to demonstrate that (i) individuals in good condition should allocate more to the sex whose fitness increases more steeply with condition and (ii) optimal sex allocation depends on the frequency distribution of conditions in the population (Charnov et al. 1978, 1981; Charnov 1979; Bull 1981; Leimar 1996). Additionally, previous models have had great predictive success in a number of empirical studies of nonmammalian taxa (e.g., Charnov et al. 1978, 1981). The application of these models to mammals, however, has been complicated by the fact that most condition-dependent sex ratio models do not include OLGs or many other demographic features of mammals (Frank 1990; for OLG models, see Charnov and Dawson 1989; Leimar 1996; Pen et al. 1999; Pen and Weissing 2002).

There are several reasons why studying sex allocation in an OLG framework can provide insight into condition-dependent sex ratios in mammals. First, it has been shown that sex ratio predictions can depend on OLGs, for example, in seasonal populations and in response to population perturbation (Werren and Charnov 1978; West and Godfray 1997). Second, with OLGs, offspring compete for reproductive opportunities with multiple cohorts, which may influence how reproductive competitiveness is measured. Finally, unlike discrete generations models, models using OLGs can reveal how different components of fitness in a long-lived organism influence the optimal sex ratio (e.g., how important are age of first reproduction and adult life span?).

In this article, we develop a model of optimal sex ratios as a function of maternal condition in a population with OLGs. The main objective of this exercise is to examine whether sex ratio predictions from discrete generations models generalize to OLGs. In addition, we examine how fitness components of long-lived offspring interact to shape optimal sex ratios and what this tells us about how to measure offspring fitness in empirical research on long-lived organisms.

Maternal Condition and Sex Allocation in a Population with Discrete Generations

We first consider a model of conditional sex ratios in a population with discrete generations for comparison with an OLG model. We use a rare-gene model to find the optimal proportion of offspring that are sons for poor (r_1) and good (r_2) mothers. A proportion, h , of females are in poor condition, and $1 - h$ are in good condition. Clutch size is b , and the mothers in good condition provide a survival advantage to both sexes of their offspring, with the advantage to sons being greater (fig. 1A). This creates a gain asymmetry between sons and daughters, with sons gaining more from good mothers than do daughters. The first-year survival rates of sons and daughters produced by mothers in poor condition are S_m and S_f , respectively. The survival rates of sons and daughters produced by mothers in good condition are $S_m\beta_m$ and $S_f\beta_f$, respectively.

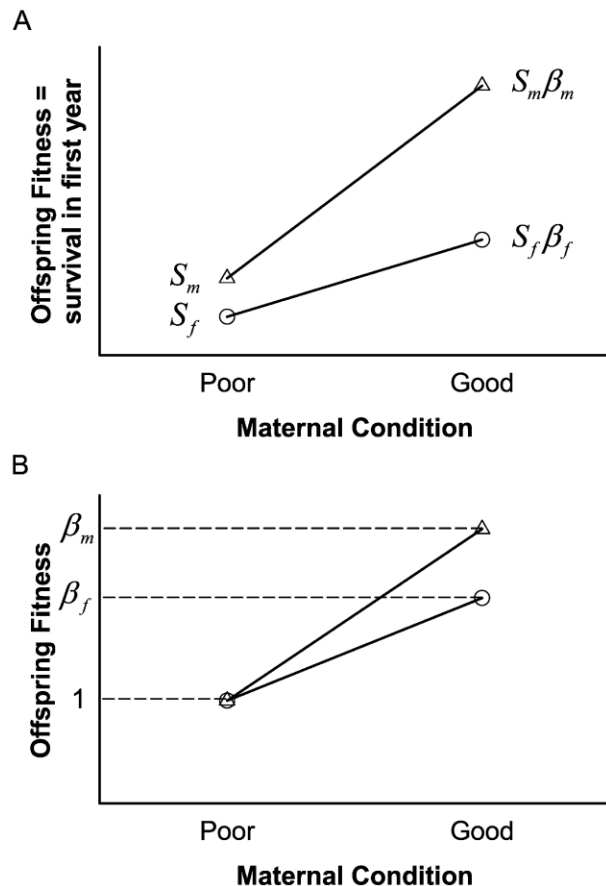


Figure 1: Maternal condition effects on offspring fitness. *A*, Juvenile survival of male (triangles) and female (circles) offspring from poor and good mothers. *B*, Offspring fitness standardized to 1 for offspring born in poor condition. Sons gain a greater advantage than daughters by being born to a mother in good condition.

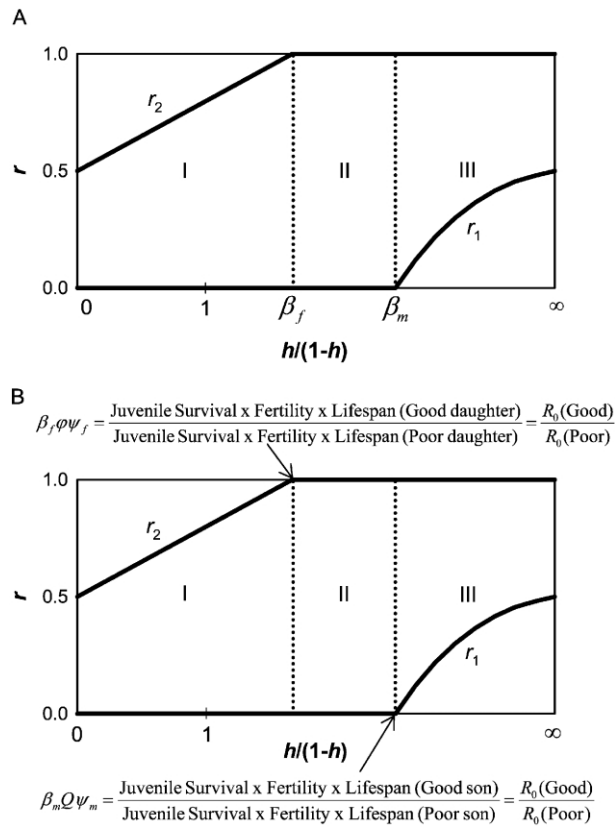


Figure 2: Optimal sex ratios (proportion of offspring that are sons) for poor (r_1) and good (r_2) mothers in three regions of $h/(1-h)$ space. *A*, Predictions from the discrete generations model. *B*, Predictions from the overlapping generations model. The optimal sex ratio depends on the within-sex ratio of offspring lifetime fitness (R_0) from good and poor mothers.

Therefore, β_m and β_f represent the relative survival advantages (the ratio) of offspring born to mothers in good condition compared with those born to mothers of poor condition (here, $\beta_m > \beta_f > 1$). Maternal condition has no influence on the condition in which their daughters reproduce (this is again assigned at random as h and $1-h$).

The model is presented in appendix A and is similar to sex ratio models in other condition-dependent systems (Charnov et al. 1978; Charnov 1979; Charnov and Dawson 1989). The final fitness equation (A1) and the sex ratio solutions (fig. 2A; table A1, eqq. [A4a], [A4b]) feature the survival advantages (β_m and β_f) but not the survival rates themselves (S_m and S_f). It is the dimensionless ratios (β_m and β_f) that determine fitness (fig. 1B).

The solutions reveal that both r_1 and r_2 cannot be optimized simultaneously as long as $\beta_m \neq \beta_f$, and one or both sex ratios must always be at a boundary (0 or 1; table

A1). The sex ratio functions ($r_2 = (1/2) + (1/2)[h/(1-h)](1/\beta_f)$, $r_1 = (1/2) - (1/2)[(1-h)/h]\beta_m$; table A1, eqq. [A4a], [A4b]) depend on the ratio of females in poor condition to females in good condition ($h/(1-h)$; fig. 2A), with three separate regions. First, when females in poor condition are rare, they produce only daughters, while good females produce a male-biased sex ratio. Second, when good females are rare, they produce only sons, while poor females produce a sex ratio < 0.5 . Third, at intermediate proportions, good females produce only sons, while poor females produce only daughters. This pattern in sex ratio biases is predicted as long as $\beta_m > \beta_f$, and the cut points between the three regions are determined by β_m and β_f .

Maternal Condition and Sex Allocation with OLGs

We extend these analyses of conditional sex allocation to populations with OLGs to examine whether OLGs per se alter the model predictions. As before, h proportion of females are in poor condition and produce a sex ratio of r_1 , whereas $1-h$ proportion of females are in good condition and produce a sex ratio of r_2 . This random assignment of breeding condition assumes that a female's birth condition does not affect the birth condition of her offspring. The age of first reproduction is 1 year, and clutch size is b . In this model, we include additional effects of maternal condition on offspring fitness components (table 1). The fecundity of a female is associated with her birth condition and not her current reproductive condition.

To explore maternal effects on sex allocation in populations with OLGs, we develop a population genetics model (app. B). We first consider the projection through time of a background population (wild-type, aa), with population dynamic equations for all females and males born under poor and good conditions separately (eqq. [B1]). We then introduce a rare, dominant mutant (Aa) into this background population and describe the population dynamics of the same life-history states (eqq. [B3]). The population dynamic equations provide a mutant fitness measure, λ_2 (the per-unit time increase of the mutant gene in a non-

Table 1: Fitness components for the overlapping generations model

Offspring sex and birth condition	First-year survival	Fertility or fecundity	Annual adult survival
Male:			
Good	$S_m \beta_m$	Q	$P_m \gamma_m$
Poor	S_m	1	P_m
Female:			
Good	$S_f \beta_f$	$b \phi$	$P_f \gamma_f$
Poor	S_f	b	P_f

growing background population), which is used to find the optimal r_1 and r_2 . As with the previous model, we find that both r_1 and r_2 cannot simultaneously have internal optima. The optimal sex ratios again depend on the ratio of the proportion of females in poor condition to the proportion of females in good condition, resulting in three regions of $h/(1 - h)$ (table 2; fig. 2B).

The solutions (table 2, eq. [1a], [1b]) are essentially unchanged from those for the rare-gene, discrete generations model (cf. table A1, eq. [A4a], [A4b]). Both solutions reflect the addition of new advantages to sons and daughters born to mothers in good condition: β_m and β_f are the familiar first-year survival advantages, Q and φ are the fertility and fecundity advantages, and ψ_m and ψ_f are adult life span advantages determined by annual adult survival advantages (γ_m and γ_f). The predicted optimal sex ratios depend on the product of these advantages in fitness components (juvenile survival advantage \times adult life span advantage \times fertility advantage). That is, the cut points for r_1 and r_2 (boundaries between regions I, II, and III) are redefined to represent the lifetime fitness advantage of being born to a mother in good condition (fig. 2B; ratio of juvenile survival \times fecundity \times adult life span for good to poor offspring). As long as the combined fitness advantage to sons is greater than the advantage to daughters ($\beta_m Q \psi_m > \beta_f \varphi \psi_f$), mothers in good condition will produce male-biased sex ratios, and mothers in poor condition will produce female-biased sex ratios. This model demonstrates that the presence of OLGs has no effect on sex allocation; it merely redefines how we measure fitness (fig. 2B). Now fitness is lifetime fitness.

Additions to the Model: General Rules for OLGs

We made two modifications to the model to explore its application to other biological situations (see app. B for more details). First, we changed the age of first reproduction (AFR) to 2 years for both males and females. The sex ratio predictions of a model with $AFR = 2$ are iden-

tical to those for $AFR = 1$. In general, we can consider an organism that reaches sexual maturity many years after birth, where annual survival each year prior to sexual maturity may differ between good and poor offspring. In this case, the total immature survival advantage would simply be the product of the yearly survival advantages (e.g., $\beta_{f1}\beta_{f2}\beta_{f3}$). Notably, a conditional advantage seen solely in first-year survival (β_{f1} or β_{m1}) would still be measured in the total juvenile survival advantage. This demonstrates the following important result: for long-lived organisms that have OLGs and that do not reproduce until many years after birth, a sex-differential conditional advantage in first-year survival alone is sufficient to predict biased sex ratios (i.e., Q , ψ_m , φ , and $\psi_f = 1$). In other words, maternal conditional effects need not be maintained until adulthood for biased sex ratios to be adaptive.

Second, we examined the situation where females breeding in good condition show an increase in fecundity compared with females in poor condition. Females in good condition were given a fecundity of $b\varphi$, where φ is the ratio of good female fecundity to poor female fecundity ($\varphi > 1$). Breeding condition is still assigned at random. This fecundity advantage to females reproducing in good condition does not affect the solutions. However, it does increase the number of sons and daughters born in good condition and redefines the region boundaries in a manner equivalent to rescaling the $h/(1 - h)$ axis by a factor of φ^{-1} .

Although we have not explored arbitrary AFR or age-specific demography or fertility, the models lead us to anticipate several generalities associated with sex ratios in nongrowing populations with OLGs. Our models demonstrate that the sex ratio solutions depend on advantages in offspring lifetime fitness (within each sex). This lifetime fitness rule is equivalent to using R_0 as the fitness measure (Charnov 1997) and should hold regardless of the particular model demography, as long as condition is assigned randomly (fig. 2B; Leimar 1996). The direction of sex ratio biases should always be predicted by the ratio of son versus

Table 2: Maternal condition and optimal sex ratios in a population with overlapping generations

Parameter space		r_1	r_2
Derivatives	regions		
I. $\frac{d\lambda_2}{dr_1} < 0, \frac{d\lambda_2}{dr_2} = 0$	$\frac{h}{1-h} < \beta_f \varphi \psi_f$	0	$\frac{1}{2} + \frac{1}{2} \frac{h}{(1-h)} \frac{1}{\beta_f \varphi \psi_f}$ (eq. [1a])
II. $\frac{d\lambda_2}{dr_1} < 0, \frac{d\lambda_2}{dr_2} > 0$	$\beta_f \varphi \psi_f \leq \frac{h}{1-h} \leq \beta_m Q \psi_m$	0	1
III. $\frac{d\lambda_2}{dr_1} = 0, \frac{d\lambda_2}{dr_2} > 0$	$\beta_m Q \psi_m < \frac{h}{1-h}$	$\frac{1}{2} - \frac{1}{2} \frac{(1-h)}{h} \beta_m Q \psi_m$ (eq. [1b])	1

Note: ψ_m is the ratio of expected adult life span of a son born in good condition (E_{mg}) to the expected adult life span of a son born in poor condition (E_{mp}), E_{mg}/E_{mp} ; $E_{mg} = 1/(1 - p_m \gamma_m)$ and $E_{mp} = 1/(1 - p_m)$. ψ_f is the ratio of expected adult life span of a daughter born in good condition (E_{fg}) to the expected adult life span of a daughter born in poor condition (E_{fp}), E_{fg}/E_{fp} ; $E_{fg} = 1/(1 - p_f \gamma_f)$ and $E_{fp} = 1/(1 - p_f)$.

daughter lifetime fitness advantages. In addition, conditional effects that impact both sexes equally (e.g., increased maternal fecundity) have little or no influence on the sex ratio predictions.

Discussion and Conclusions

We have developed a model of optimal sex allocation when maternal condition varies for populations with OLGs. It takes into account a number of biological scenarios, and its flexibility (e.g., altering various aspects of offspring fitness and population demography) should be of great use for future theoretical extensions. The life-history aspects incorporated in our models include maternal effects on all components of offspring lifetime fitness (R_0), delayed age of first reproduction, and condition-based fecundity benefits. Our model has demonstrated that the presence of OLGs per se has no effect on the sex ratio predictions. Of course, this generalization must be accompanied by the caveat that many social and reproductive characteristics often thought to impact sex ratios operate only when generations overlap (e.g., daughters may remain near and interfere with their mother's future reproduction).

The model we have developed in this article also advances our views on how fitness effects in offspring shape optimal sex ratios. Similar to other sex ratio models, we found that the optimal sex ratios depend on the relative within-sex advantages of maternal condition and that absolute differences in offspring fitness between the sexes did not matter (Charnov 1979). In addition, offspring juvenile survival, adult life span, and fertility combine to redefine offspring fitness as lifetime fitness or R_0 . When one offspring sex gains more in lifetime fitness from being born to good-condition mothers (e.g., males: $\beta_m Q \psi_m > \beta_f \varphi \psi_f$), that sex will be overrepresented in the offspring of those mothers. The importance of lifetime fitness has previously been argued for maternal-condition-based sex ratios by Leimar (1996). Here, we show that offspring lifetime fitness is the product of three measurable fitness components (juvenile survival \times adult life span \times annual fertility; Charnov 1997).

This lifetime fitness rule indicates which aspects of offspring phenotype and life history should be emphasized in empirical research on sex ratios. In the conceptual model of Trivers and Willard (1973), maternal condition affected the reproductive success of sons more than that of daughters (assumption 3). This is captured in our model by the fertility and fecundity variables (Q and φ). This emphasis on adult reproductive success (fertility and fecundity) has led to much attention being placed on the second T-W assumption that maternal effects are maintained until adulthood. Here, we've confirmed that neither of these assumptions needs to be met in order for

condition-dependent sex ratios to be adaptive. Fertility advantages represent only one of the three fitness components in the lifetime fitness of each sex of offspring. The other two are juvenile survival and adult life span. If maternal condition influences only offspring survival from weaning to sexual maturity, this is potentially sufficient to lead to biased sex ratios. In addition, if any of the lifetime fitness components combine to provide a sex-differential advantage with condition, our model predicts condition-dependent biased sex ratios.

Our model also illustrates how opposing advantages to offspring fitness components might select for unbiased sex ratios based on maternal condition. For example, sons may gain more in fertility from maternal condition (i.e., T-W hypothesis), but if daughters gain equally more in juvenile survival, this could negate a benefit for biased sex ratios. Therefore, empirical research on conditional sex ratios (including T-W) should attempt to measure all three components of lifetime fitness (juvenile survival, adult life span, and fertility) rather than focusing on fertility alone (for a similar argument, see Leimar 1996). This is difficult in practice but is essential for an accurate prediction of offspring sex ratios.

Finally, we do not wish to leave the impression that age-structured life histories never show the potential to select for facultative sex ratios due to age structure itself, only that a maternal condition effect may not change with OLGs. At least two age-structured facultative effects have been studied. Short-lived organisms in seasonal environments with small overlap in generations (i.e., across-season age structure) may have adaptive seasonal shifts in sex ratio (Werren and Charnov 1978). These shifts are known for several species (Seger 1983; Conover and Heins 1987) and may occur in mammals (e.g., McShea and Madison 1986). As a second example, long life in mammals is often correlated with a litter size of 1. If a male offspring imposes a different mortality rate on the mother than a daughter does, a shift in offspring sex is predicted with the mother's age such that the sex imposing the lower mortality should be born to younger mothers (Charnov 1982, p. 96). This is an age-structured prediction even for mothers of the same quality because mothers showing the age shift will increase their own life span. This effect seems not to be consistently observed in mammals (Hewison et al. 2002).

We imagine some logical extensions of the model that take into account further potential biological complications. Some of these extensions might help elucidate the inconsistent sex ratios of mammals. First, adding an interaction between maternal condition and a daughter's adult reproductive condition may alone create a relative advantage for daughters (Leimar 1996), although it remains unclear as to when this would overcome a son's relative advantage and lead to production of daughters by

mothers in good condition. Second, we could include small clutch size effects and sex-specific quality versus offspring size curves to examine whether a mother with adequate resources should have one high-quality son or two average daughters (Williams 1979). Third, there may be costs or constraints of sex ratio manipulation (e.g., to fecundity; Pen and Weissing 2002). If the sex ratio itself can be moved only in the region of, say, 0.35–0.65, we expect that boundary sex ratios would be at the allowable extremes. Finally, multiple forces (e.g., conditional, social) may impact offspring fitness in mammals and may interact to accentuate or cancel the benefits of sex ratio biases (Cockburn et al. 2002). For example, in some mammals, competition with daughters may be important in shaping sex ratios at high population density or in young mothers (local resource competition; Clark 1978), while maternal

condition becomes more important for sex ratios at low density or in older mothers (e.g., van Schaik and Hrdy 1991; Kruuk et al. 1999; Isaac et al. 2005). The OLG model we have presented in this article can provide the foundation for models that examine these interacting effects and, potentially, shed light on the diversity of natural sex ratios observed in mammals.

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APPENDIX A

Discrete Generations

Our model follows closely the original argument introduced by Shaw and Mohler (1953). We count the contribution of genes to grandchildren by a single mutant mother who produces sex ratios of \hat{r}_1 and \hat{r}_2 in a population of wild-type mothers producing r_1 and r_2 . Suppose N wild-type mothers (plus the mutant) each produce sons and daughters. Subsequently, the offspring reproduce, the population of new adults produces K fertilized zygotes (grandchildren), and K grandchildren have $2K$ haploid chromosome sets (HCS), K of which come from males and K of which come from females. The mutant mother's fitness (W) is the proportion of HCS that came from her offspring.

If N is large, the mutant mother's contribution to grandchildren through sons and daughters is

$$K \frac{h\hat{r}_1 bS_m + (1-h)\hat{r}_2 bS_m \beta_m}{N[hr_1 bS_m + (1-h)r_2 bS_m \beta_m]},$$

$$K \frac{h(1-\hat{r}_1) bS_f + (1-h)(1-\hat{r}_2) bS_f \beta_f}{N[h(1-r_1) bS_f + (1-h)(1-r_2) bS_f \beta_f]}.$$

The total genetic contribution of the mutant mother to grandchildren is then

$$W = \left[\frac{h\hat{r}_1 + (1-h)\hat{r}_2 \beta_m}{hr_1 + (1-h)r_2 \beta_m} + \frac{h(1-\hat{r}_1) + (1-h)(1-\hat{r}_2) \beta_f}{h(1-r_1) + (1-h)(1-r_2) \beta_f} \right] \frac{K}{N}. \quad (\text{A1})$$

Without loss of generality, we also set $K/N = 1$.

Because a wild-type organism has $W = 2$, a mutant will invade the population if it has $W > 2$. The sex ratios r_1 and r_2 are evolutionarily stable if there are no mutant values (\hat{r}_1 , \hat{r}_2) that make $W > 2$. At the evolutionarily stable strategy (ESS) conditions: (1) W is maximized with respect to \hat{r}_1 and \hat{r}_2 , (2) $\hat{r}_1 = r_1$, and $\hat{r}_2 = r_2$, and (3) $W = 2$. To find the ESS, we consider the derivatives $dW/d\hat{r}_1$ and $dW/d\hat{r}_2$, when $\hat{r}_1 = r_1$ and $\hat{r}_2 = r_2$. The derivatives are

$$\frac{dW}{d\hat{r}_1} = \frac{h}{hr_1 + (1-h)r_2 \beta_m} + \frac{-h}{h(1-r_1) + (1-h)(1-r_2) \beta_f}, \quad (\text{A2a})$$

$$\frac{dW}{d\hat{r}_2} = \frac{(1-h)\beta_m}{hr_1 + (1-h)r_2 \beta_m} + \frac{-(1-h)\beta_f}{h(1-r_1) + (1-h)(1-r_2) \beta_f}. \quad (\text{A2b})$$

If we set $M = hr_1 + (1-h)r_2\beta_m$ and $F = h(1-r_1) + (1-h)(1-r_2)\beta_p$, we find

$$\frac{dW}{d\hat{r}_1} = \frac{1}{M} - \frac{1}{F}, \quad (\text{A3a})$$

$$\frac{dW}{d\hat{r}_2} = \frac{\beta_m}{M} - \frac{\beta_f}{F}. \quad (\text{A3b})$$

With $\beta_m > \beta_p$, these two derivatives cannot simultaneously equal 0. Consideration of equations (A3) reveals that there are three possible situations (see table A1; fig. 2A).

Table A1: Maternal condition and optimal sex ratios in a population with discrete generations

Derivatives	Parameter space		
	regions	r_1	r_2
I. $\frac{dW}{d\hat{r}_1} < 0, \frac{dW}{d\hat{r}_2} = 0$	$\frac{h}{1-h} < \beta_f$	0	$\frac{1}{2} + \frac{1}{2} \frac{h}{(1-h)} \frac{1}{\beta_f}$ (eq. [A4a])
II. $\frac{dW}{d\hat{r}_1} < 0, \frac{dW}{d\hat{r}_2} > 0$	$\beta_f \leq \frac{h}{1-h} \leq \beta_m$	0	1
III. $\frac{dW}{d\hat{r}_1} = 0, \frac{dW}{d\hat{r}_2} > 0$	$\beta_m < \frac{h}{1-h}$	$\frac{1}{2} - \frac{1}{2} \frac{(1-h)}{h} \beta_m$ (eq. [A4b])	1

APPENDIX B

Overlapping Generations

To examine condition-dependent sex ratios in a population with overlapping generations, we first describe the background (wild-type, aa) population using population dynamic equations. We count the number of females born under poor condition ($n_p(t)$), females born under good condition ($n_g(t)$), males born under poor condition ($n_p^*(t)$), and males born under good condition ($n_g^*(t)$). In stable-age distribution,

$$n_p(t+1) = n_p(t)p_f + n_p(t)h(1-r_1)bS_f + n_g(t)h(1-r_1)b\varphi S_f = \lambda_1 n_p(t), \quad (\text{B1a})$$

$$n_g(t+1) = n_g(t)p_{\gamma_f} + n_p(t)(1-h)(1-r_2)bS_f\beta_f + n_g(t)(1-h)(1-r_2)b\varphi S_f\beta_f = \lambda_1 n_g(t), \quad (\text{B1b})$$

$$n_p^*(t+1) = n_p^*(t)p_m + n_p(t)hr_1bS_m + n_g(t)hr_1b\varphi S_m = \lambda_1 n_p^*(t), \quad (\text{B1c})$$

$$n_g^*(t+1) = n_g^*(t)p_{\gamma_m} + n_p(t)(1-h)r_2bS_m\beta_m + n_g(t)(1-h)r_2b\varphi S_m\beta_m = \lambda_1 n_g^*(t), \quad (\text{B1d})$$

where λ_1 is the dominant eigenvalue of the transition matrix. The population is growing when $\lambda_1 > 1$ and stable when $\lambda_1 = 1$. In order to find λ_1 , we find the characteristic equation of the transition matrix. We assume a nongrowing background population ($\lambda_1 = 1$), and so we must also assume that at least one variable in λ_1 is density dependent. We propose that S_f is the most likely variable to carry the density dependence and solve accordingly:

$$S_f = \frac{1 - p_f}{b[h(1-r_1) + (1-h)(1-r_2)\beta_f\varphi\psi_f]}, \quad (\text{B2})$$

where $\psi_f = (1-p_f)/(1-p_{\gamma_f})$. In practice, density dependence could be anywhere in bS_f .

Now we consider a mutant (Aa) that is introduced into the population. When the mutant is rare, all mutants mate only with wild-type individuals ($Aa \times aa$) so that half of all offspring produced by mutants are themselves mutants. Mutant offspring arise through mutant females mating with wild-type males and mutant males mating with wild-type females. The mutant produces offspring sex ratios \hat{r}_1 and \hat{r}_2 . As with the background population, we can write out the growth equations for the mutants (a circumflex denotes mutant parameters) as follows:

$$\begin{aligned}\hat{n}_p(t+1) &= \hat{n}_p(t)p_f + [\hat{n}_p(t) + \hat{n}_g(t)\varphi] \left[\frac{1}{2}h(1 - \hat{r}_1)bS_f \right] \\ &+ [n_p(t) + n_g(t)\varphi] \left[\frac{1}{2}h(1 - r_1)bS_f \right] \left[\frac{\hat{n}_p^*(t) + \hat{n}_g^*(t)Q}{n_p^*(t) + n_g^*(t)Q} \right],\end{aligned}\quad (\text{B3a})$$

$$\begin{aligned}\hat{n}_g(t+1) &= \hat{n}_g(t)p_{\hat{\gamma}_f} + [\hat{n}_p(t) + \hat{n}_g(t)\varphi] \left[\frac{1}{2}(1 - h)(1 - \hat{r}_2)bS_f\beta_f \right] \\ &+ [n_p(t) + n_g(t)\varphi] \left[\frac{1}{2}(1 - h)(1 - r_2)bS_f\beta_f \right] \left[\frac{\hat{n}_p^*(t) + \hat{n}_g^*(t)Q}{n_p^*(t) + n_g^*(t)Q} \right],\end{aligned}\quad (\text{B3b})$$

$$\begin{aligned}\hat{n}_p^*(t+1) &= \hat{n}_p^*(t)p_m + [\hat{n}_p(t) + \hat{n}_g(t)\varphi] \left[\frac{1}{2}h\hat{r}_1bS_m \right] \\ &+ [n_p(t) + n_g(t)\varphi] \left[\frac{1}{2}hr_1bS_m \right] \left[\frac{\hat{n}_p^*(t) + \hat{n}_g^*(t)Q}{n_p^*(t) + n_g^*(t)Q} \right],\end{aligned}\quad (\text{B3c})$$

$$\begin{aligned}\hat{n}_g^*(t+1) &= \hat{n}_g^*(t)p_{\gamma_m} + [\hat{n}_p(t) + \hat{n}_g(t)\varphi] \left[\frac{1}{2}(1 - h)\hat{r}_2bS_m\beta_m \right] \\ &+ [n_p(t) + n_g(t)\varphi] \left[\frac{1}{2}(1 - h)r_2bS_m\beta_m \right] \left[\frac{\hat{n}_p^*(t) + \hat{n}_g^*(t)Q}{n_p^*(t) + n_g^*(t)Q} \right].\end{aligned}\quad (\text{B3d})$$

For the mutant to invade, the dominant eigenvalue of the mutant population matrix, λ_2 , must be greater than that of the background population (λ_1). Because we assume a nongrowing background population ($\lambda_1 = 1$), λ_2 must be >1 . The sex ratios r_1 and r_2 are evolutionarily stable if there are no mutant values (\hat{r}_1, \hat{r}_2) that make $\lambda_2 > \lambda_1$. At the ESS conditions, (1) λ_2 is maximized with respect to \hat{r}_1 and \hat{r}_2 , (2) $\hat{r}_1 = r_1$ and $\hat{r}_2 = r_2$, and (3) $\lambda_2 = 1$.

To find λ_2 , we must find the characteristic equation of the mutant matrix $\{\mathbf{A}_2\}$. Equations (B3) can be written in terms of R , the adult sex ratio weighted by the fertility advantage of good males and females:

$$R = \frac{n_p(t) + n_g(t)\varphi}{n_p^*(t) + n_g^*(t)Q}. \quad (\text{B4})$$

The mutant matrix, $\{\mathbf{A}_2\}$, is then

$$\begin{bmatrix} p_f + \frac{1}{2}h(1 - \hat{r}_1)bS_f & \frac{1}{2}h(1 - \hat{r}_1)b\varphi S_f & \frac{1}{2}h(1 - r_1)bS_f R & \frac{1}{2}h(1 - r_1)bS_f R Q \\ \frac{1}{2}(1 - h)(1 - \hat{r}_2)bS_f\beta_f \left[p_{\hat{\gamma}_f} + \frac{1}{2}(1 - h)(1 - \hat{r}_2)b\varphi S_f\beta_f \right] & \frac{1}{2}(1 - h)(1 - \hat{r}_2)bS_f\beta_f R & \frac{1}{2}(1 - h)(1 - \hat{r}_2)bS_f\beta_f R Q & \\ \frac{1}{2}h\hat{r}_1bS_m & \frac{1}{2}h\hat{r}_1b\varphi S_m & p_m + \frac{1}{2}hr_1bS_m R & p_m + \frac{1}{2}hr_1bS_m R Q \\ \frac{1}{2}(1 - h)\hat{r}_2bS_m\beta_m & \frac{1}{2}(1 - h)\hat{r}_2b\varphi S_m\beta_m & \frac{1}{2}(1 - h)r_2bS_m\beta_m R & \left[p_{\gamma_m} + \frac{1}{2}(1 - h)r_2bS_m\beta_m R Q \right] \end{bmatrix}.$$

Assuming the background population is in stable-age distribution, we use equations (B1c) and (B1d) to find

$$R = \left[\frac{hr_1bS_m}{1 - p_m} + \frac{(1 - h)r_2bS_m\beta_m Q}{1 - p_m\gamma_m} \right]^{-1}.$$

We also substitute equation (B2) into the matrix for S_f so that the same density dependence applies to the mutant.

From the characteristic equation of $\{\mathbf{A}_2\}$, we find λ_2 . To find the ESS, we consider the derivatives $d\lambda_2/d\hat{r}_1$ and $d\lambda_2/d\hat{r}_2$, when $\hat{r}_1 = r_1$ and $\hat{r}_2 = r_2$, and set these equal to 0. We performed the following calculations (see app. C in the online edition of the *American Naturalist*): (1) Use the background transition matrix to solve for S_f . (2) Calculate the characteristic equation of $\{\mathbf{A}_2\}$. (3) Take the derivative of λ_2 , with respect to \hat{r}_1 and \hat{r}_2 . (4) Apply ESS conditions: $\hat{r}_1 = r_1$, $\hat{r}_2 = r_2$, and $\lambda_2 = \lambda_1 = 1$. (5) Solve for r_1 and r_2 when $d\lambda_2/d\hat{r}_1 = 0$ and $d\lambda_2/d\hat{r}_2 = 0$, respectively. (6) Confirm that both derivatives cannot be optimized simultaneously (cannot equal 0 simultaneously). (7) Solve for r_1 with $r_2 = 1$. Solve for r_2 with $r_1 = 0$. These are the final solutions. (8) Confirm the assumptions in step 7 that if r_1 has an internal optimum, then $r_2 = 1$ and if r_2 has an internal optimum, then $r_1 = 0$ (for $\beta_m Q \psi_m > \beta_f \varphi \psi_f$).

Additional Model Modifications

Age of First Reproduction of 2 Years. To modify the model for age of first reproduction of 2 years rather than 1 year, we track (1) first-year females (daughters produced by females ≥ 2 years old \times juvenile survival from the previous year) and (2) ≥ 2 -year-old females (survival of first-year and ≥ 2 -year-old females from the previous year). Survival after the first year is equal to adult survival. We treat males in a comparable fashion. We assumed that adult survival does not differ between offspring born in different conditions, and the only advantage to offspring born in good condition is a first-year survival advantage to sons. The process of finding the ESS sex ratios follows the same steps as before.

Females Reproducing in Good Condition Have a Fecundity Advantage. To give a fecundity advantage to females reproducing in good condition, we assign a fecundity of $b\varphi$ to the $1 - h$ proportion of females in good condition, where $\varphi > 1$. The fecundity advantage is due only to the condition in which the female is reproducing that year and is not influenced by the condition in which she was born. Advantages to offspring from being born to a mother in good condition are seen only in juvenile survival, with $\beta_m > \beta_f > 1$. We use one equation each to count females and males in the population. The process of finding the ESS sex ratios follows similar steps as before.

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